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Illustrations of Some Lycopodium Gametophytes

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In a recent number of this JOURNAL¹ Hollis Koster described the hitherto unknown gametophytes of some species of *Lycopodium* and discussed briefly the history of our acquaintance with the sexual generation of the club mosses. He suggests that, since these plants are still unknown for many species, and stations for others are few, field botanists might well give attention to them. He believes that the gametophytes are not so rare as the collections would suggest; that systematic search should uncover much more material. With this opinion the writer agrees. Members of the staff of the Department of Botany at Cornell University have been searching for and collecting club moss gametophytes for the past 15 years with marked success. Information obtained by them, with illustrations from their material, together with illustrations of Koster's plants and his published descriptions, should assist others in obtaining these well-hidden plants.

It has long been known that there are two markedly different types of gametophyte in the genus: the green, surface-living, rapidly developing, short-lived, and minute form and the nongreen, subterranean, slowly developing, long-lived, and much larger form.

¹ 31: 53-58. 1941.

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The first type is well described by Koster and is here illustrated in Plate 1, *Lycopodium alopecuroides*. (The drawings were made from material collected by him and sent to Cornell University.) His paper should be referred to for details of description and for a general discussion of habitat and occurrence. It will suffice here to emphasize the fact that the full-grown plant is only 1 to 2 mm. in diameter, merely a green speck on the humus or decaying vegetation of the swamp, and that most careful search is therefore necessary. The plants can be most readily found, of course, when they have borne young sporophytes (Plate 1, fig. c), which, being larger, are more easily seen.

The Cornell group have no acquaintance with this type in the field, because the species possessing this form are absent or very rare in the regions where field studies are readily made. The second type (Plates 2, 3, 4) has been found by them in considerable abundance at a large number of stations chiefly in and near the Cayuga Lake Basin in west-central New York. The following species have been collected: *L. obscurum*, *L. clavatum*, *L. complanatum*, *L. lucidulum*, and *L. annotinum*, the first species most frequently, the last two rarely. Collections of this type in the northeastern states by other botanists are referred to by Koster. None has yet been found for *L. tristachyum*, but this species is rare in the regions searched.

The gametophytes of this second type, being subterranean, are of course to be located only by the finding of the young sporophytes, which remain for some time—in some cases, at least, up to several years—attached to the gametophytes which bear them. As will be seen in Plates 2 to 4, the young sporophytes when first appearing above ground superficially resemble *Polytrichum*, but differences in aspect as well as in details of structure will

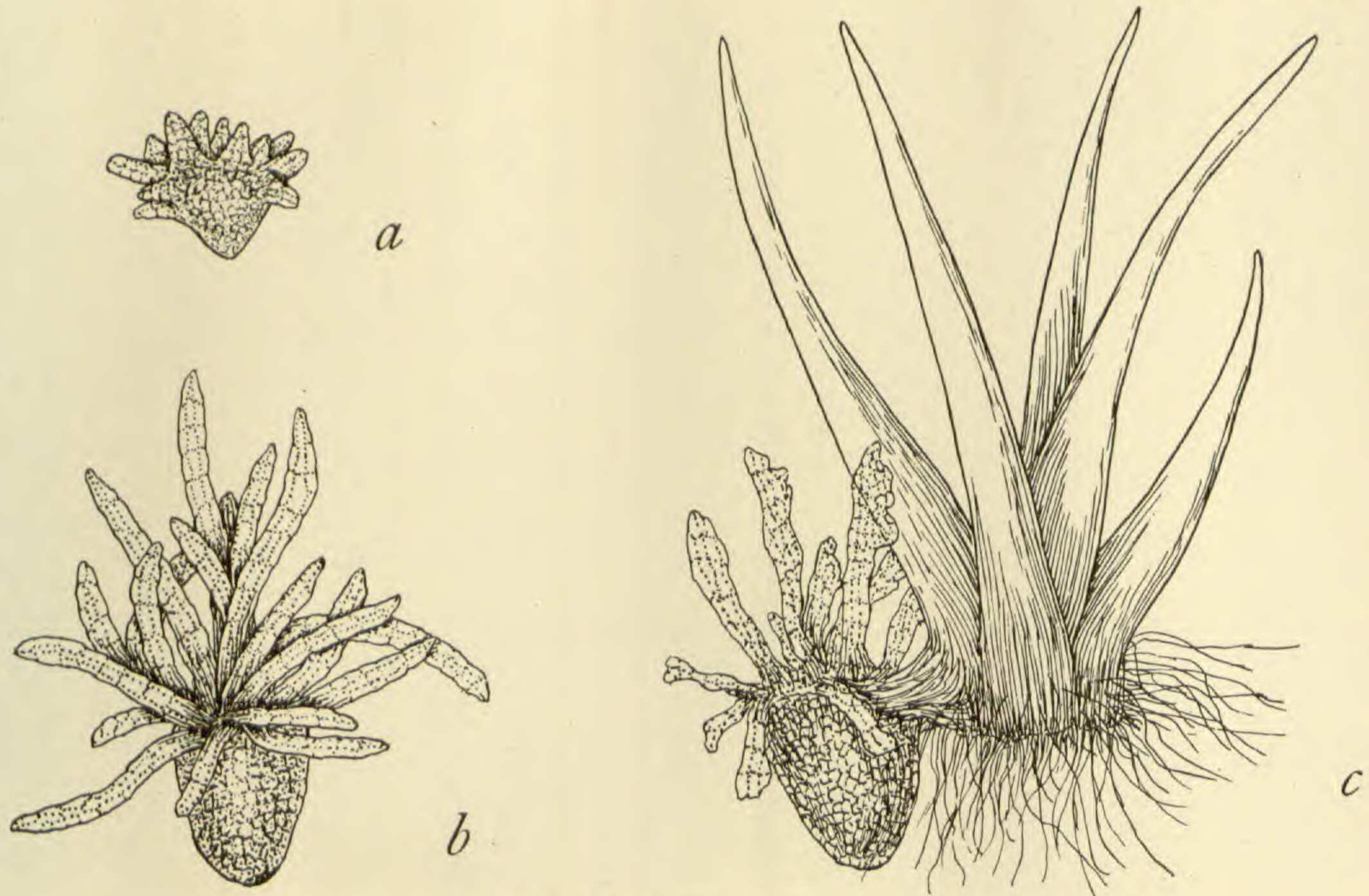
quickly be seen. As the sporophyte increases in size, changes of leaf form and arrangement, stem position, branching, etc., indicate the species represented.²

Attempts have been made to learn in what habitats to search for these subterranean plants, but the localities found seem to have little in common. It can be said definitely, however, that, as Koster learned for the swamp species with their surface-living gametophytes, it is useless to search where mature and fruiting plants are abundant; the sexual plants have not been found where mature plants are numerous and only rarely are they discovered even near the borders of colonies. Nearly all have been found where no mature plants exist in the neighborhood, and sometimes none can be found in the same woodland areas.

It is evident, therefore, that the searcher should look everywhere except where, at first thought, he thinks the plants will probably be found. The explanation for this peculiarity of distribution lies perhaps largely in the fact that habitat conditions which are suitable for the growth of mature plants are not suitable for spore germination and the development of the delicate gametophyte. The great abundance of spores formed and the lightness of these spores make certain a broad and general distribution, but only where conditions of ground surface are right do the gametophytes develop.

In considering the conditions favorable to growth of these sexual plants it should be remembered that the gametophytes lie at varying depths below the surface of the soil—usually 3 to 10 cm., but ranging from 1 to 20 cm.; that they have been developing there for 10 to 25 years, during which time humus has increased above them. Most individuals are found in the lower parts of

² Details of description and consideration of comparative morphology of the gametophytes and young sporophytes of the species listed above will be presented in a later paper.

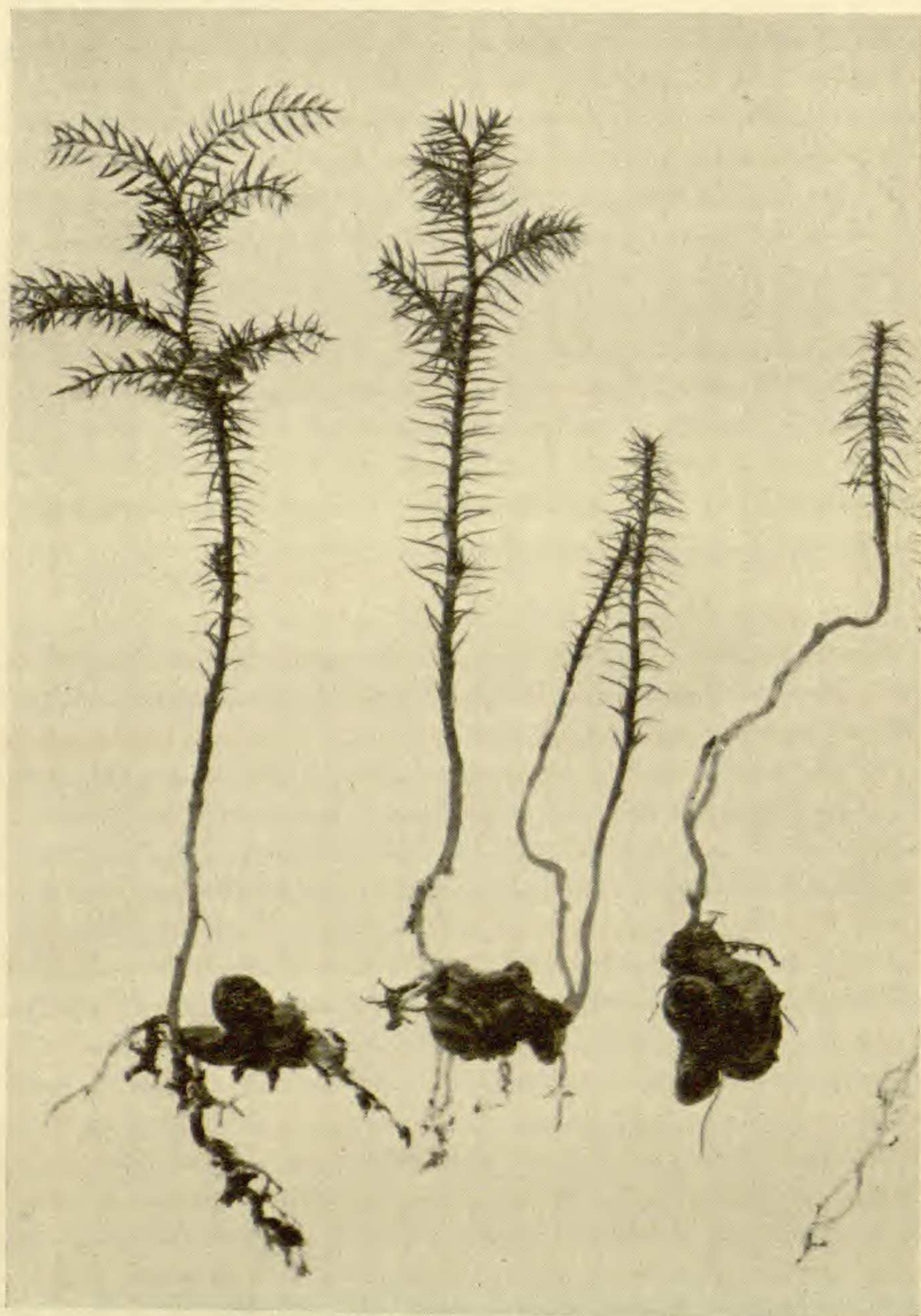


LYCOPodium ALOPECUROIDES

the humus layer, although some have been found 2 or 3 cm. deep in the soil below the humus layer. Where most abundant they occur in small pockets in the forest floor, chiefly on the line between the humus and the soil below. In such areas this line is marked by charcoal from a forest fire. It seems possible that a forest fire, especially one that follows timber-cutting, provides a highly favorable spore-bed and perhaps other favorable conditions.

The spores may reach the level where the gametophytes are found in any number of ways: washing down by rain through the soil crevices; burial by insects or larger animals; any type of disturbance of the soil surface. The fact that so many are found at the base of the humus layer suggests, of course, that the spores are washed down as far as the soil is freely porous. The abundance of gametophytes at this level when a charcoal layer is present suggests also that perhaps the most favorable spore-bed is one where little or no humus is present, that the spores are blown in soon after the fire, and that the gradual building up of humus above the spores as they begin to germinate provides the best growing conditions. This suggestion is supported by the history of development of the plants: The spores do not germinate for 2 or 3 years; a period of 10 to 15 years is required for development of the gametophyte to maturity, time sufficiently long for the accumulation of the humus layer over the plants. In two areas where gametophytes have been found most abundantly the trees and shrubs range in age from 5 to 25 years and obviously had grown after a forest fire following timber-cutting.

The habitats known to the Cornell group are chiefly these: Young upland deciduous forest, apparently cleared in recent years and growing rapidly (for all species of *Lycopodium* listed); white pine forest, dry and usually open (for *L. complanatum* chiefly); open gravelly knolls and abandoned fields with *Hamamelis* and *Rhus*



LYCOPodium OBSCURUM

(for *L. complanatum*) ; low red-maple forest about peat bogs (for *L. obscurum*). These habitats suggest that changes in light, soil type, and temperature as a result of the opening and gradual closing of the forest may directly or indirectly provide favorable growth conditions for these plants. Possibly forest fires make these conditions even more favorable.

Only few out of many apparently perfectly favorable locations will be found to have gametophytes, and some seemingly most unlikely areas may be found to have a few. Doubtless, also, favorable growing seasons must exist for the early stages of development and for later survival. It is, naturally, impossible to determine the age of the gametophytes in a certain area and therefore to ascertain the seasonal conditions at germination time, which may have been 10 to 25 years earlier. Absence of plants from suitable localities may of course be due to absence of spores carried to the region when soil conditions were right; but when these regions are those where fruiting sporophytes are frequent, it is probable that unfavorable growing conditions have exterminated the plants at some period during the years of development. The drought of the summer of 1930 killed great numbers of gametophytes of *L. clavatum* and *L. obscurum* at the first station known in the Cayuga Lake Basin where these plants were abundant; the humus of the forest floor was dry over so long a period that only occasional individuals survived—even the well-established young sporophytes, whether still attached to the gametophytes or living independently, being killed. The dry summer of 1940 destroyed a large part of the plants at the second station known. If such destruction occurs before the sporophytes appear above ground, the existence of a colony of plants can of course never be known.

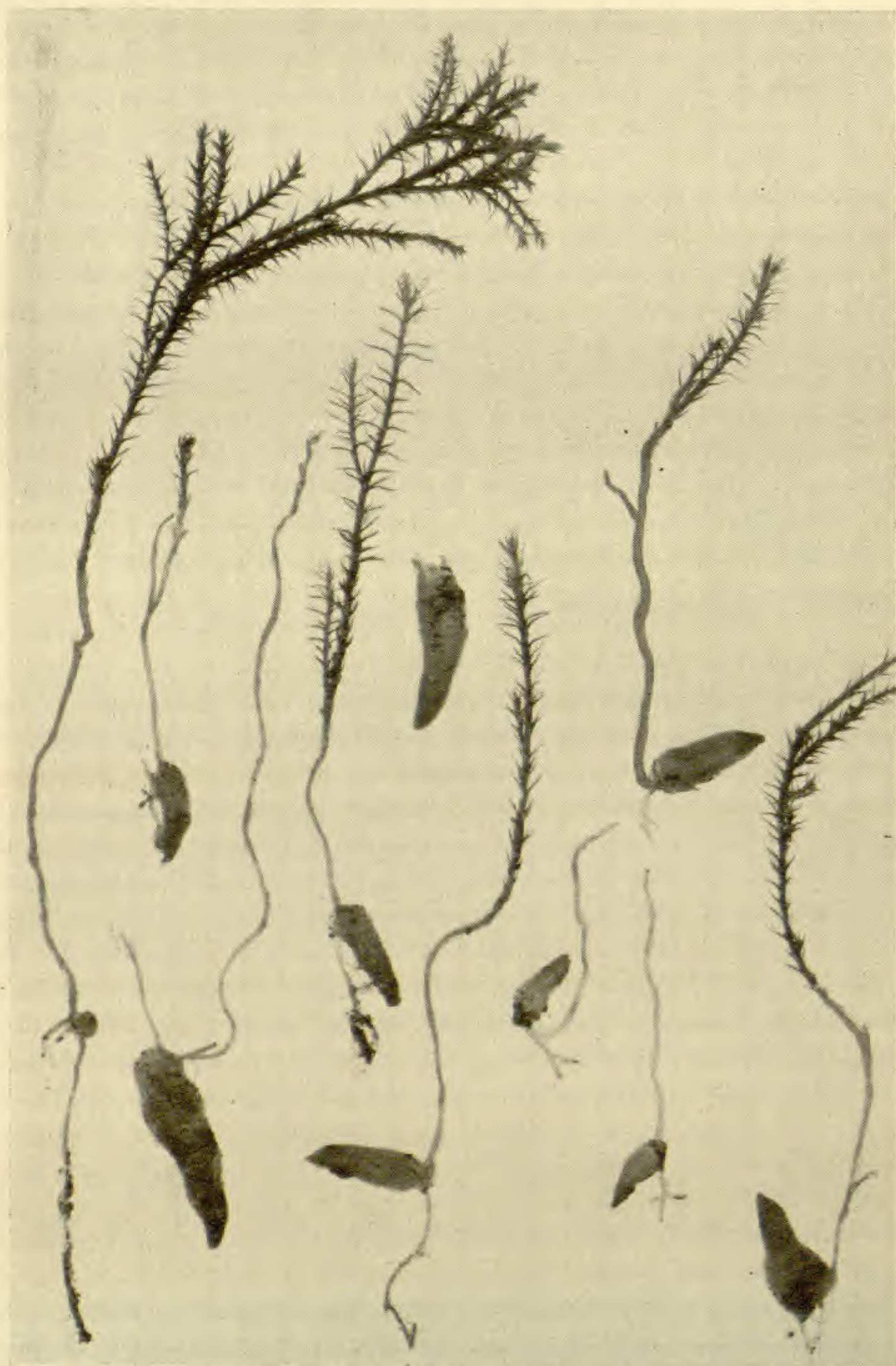
When one or more young sporophytes have been found, the area should be considered favorable for gametophytes



LYCOPodium LUCIDULUM

and the search made intensive, especially for sporophytes just appearing above ground. All sporophytes should be dug carefully from the soil, although usually the gametophyte, if present, is firmly attached and not easily broken off. If several plants occur close together, especially in little hollows or beside rotting stumps or logs, the soil about them should be removed and sifted for gametophytes which as yet have borne no sporophytes. These may be found in varying size and stage of development. It is clear either that germination of spores occurs at different times, perhaps even years apart, or that the growth rate of gametophytes varies greatly, for plants of different sizes and ages can sometimes be found together; the smallest which can be readily found, 2 or 3 mm. in diameter, as yet without sex organs; the oldest up to 1 or 2 cm. in diameter, bearing sporophytes one to several years old. Sex organs are borne years before the gametophyte reaches full size and may continue to be borne for at least a few years after embryos are formed. More than one sporophyte may be borne by a gametophyte in the same year or in different years: two are common; three to five occasional; and even seven well-grown sporophytes have been found on one large gametophyte. This condition is in strong contrast with that in common ferns, where only one embryo is formed and the gametophyte dies soon after the sporophyte is established.

The length of life of the gametophyte after embryo formation varies greatly: It will be found that in favorable habitats nearly all young sporophytes showing above ground are attached to gametophytes; but where soil conditions are poor, or after drought, only a few may have the sexual generation still present. Although the gametophyte apparently does not commonly persist more than two or three years after it bears a sporophyte, a few sporophytes of *L. obscurum* that were at least five years old



LYCOPODIUM COMPLANATUM

have been found still attached to healthy gametophytes. These gametophytes were the largest collected and were apparently still growing. Sporophytes that are clearly sporelings should therefore be investigated for possible gametophytes, even if they seem to be so large that the chances of finding sexual plants are small.

The gametophytes of a given locality will continue to form sporophytes over a period of years, limited perhaps to about 10 as a maximum. This distribution of the crop is doubtless partly related to the different rate of development of the gametophytes, and partly to the continued development of sex organs over a period of years, whether embryos are formed or not.

Among the species studied, *L. obscurum* is found most frequently and in most varied habitats. It is apparently the most resistant to unfavorable growing conditions, surviving drought when other species, especially *L. clavatum*, are killed.

In form the gametophytes of the various species differ considerably. In *L. complanatum* the plant is carrot-shaped (Plate 4), with the sex organs in a crown on the larger end. In *L. lucidulum* it is roughly cylindrical (Plate 3), with a "rolled" appearance given by a longitudinal furrow or crease. The sex organs seem always to be borne at one end. The other species (*L. obscurum*, *L. clavatum*, *L. annotinum*) have gametophytes which much resemble each other, and probably cannot be distinguished from one another until they reach full size, in some cases not even then unless they have sporophytes that can be named. All of these when very small are club-shaped, but the thicker end soon spreads out, forming a button-like disk which grows at its margin and rolls upward and inward slightly. The sex organs are borne just at the inside of the margin. As the diameter increases, the sides tend to curl upward or downward, the

plant becoming furrowed and saddle-shaped. With continued growth the curling continues and the plant becomes complexly convoluted, somewhat resembling a "walnut meat." Some individuals become lobed and remain nearly flat (Plate 2).

In *L. clavatum* the gametophyte averages smaller than that of either of the other species, and usually does not become convoluted to any extent, remaining disk-shaped. In *L. annotinum* it becomes deeply furrowed; but as it grows larger, it remains simple, retaining the saddle shape, and does not develop lateral convolutions. The sides of the "saddle" spread apart so that the plant has apparent bilateral symmetry and may appear dichotomous.

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EXPLANATION OF PLATES

PLATE 1. *Lycopodium alopecuroides*. *a, b*, young gametophyte; *c*, mature gametophyte with young sporophyte. ($\times 20$.)

PLATE 2. *Lycopodium obscurum*. Gametophytes bearing well-grown sporophytes, the oldest beginning to show habit of mature plant. One gametophyte has three sporophytes. ($\times 1$.)

PLATE 3. *Lycopodium lucidulum*. Gametophytes and young sporophytes. The specimen at the left is a young sporophyte borne by a gemma, not by a gametophyte; the absence of a primary root and the stouter, less tapering stem distinguish a young plant of this type from one of the same size which has arisen by sexual reproduction—cf. the specimen next to it. ($\times 1.7$.)

PLATE 4. *Lycopodium complanatum*. Gametophytes and young sporophytes. The largest sporophyte (specimen at the left) is no longer attached to a gametophyte but shows the knoblike "foot" or haustorial organ by which it was earlier attached. ($\times 1$.)